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Geographical and ecological
determinants of
distribution patterns ~

The study of animal distribution in southern Africa has not yet reached a stage where much factual material is available for a general treatment of the environmental control of distribution patterns. None the less, the discussion of general problems even at this stage is desirable, if only to attempt to reach some clarity about the nature of the problems confronting us. The purpose of this paper is to discuss four factors which are generally considered to determine distribution patterns, and about which at least some information is available, namely sea barriers, temperature, rainfall and vegetation. To avoid excessive complication, the scope of this paper is limited to a consideration of terrestrial animals only.

Sea Barriers

At present the effect of sea barriers on animal distribution in southern Africa is obvious enough. However, the fact that the coastline of southern Africa dates only from the first half of the Cretaceous (King 1958) should be borne in mind when dealing with the distribution of more ancient groups. Past excesses in palaeogeographical speculation have led to a present diffidence about the question of former continental connections, particularly amongst workers in the northern hemisphere, as was recently shown in the Royal Society's discussion on the southern temperate zone (*Proc. roy. Soc. Lond.*, B, vol. 152, 1960, no. 949). But however risky it may be to indulge in geographical speculation on the basis of animal distribution, workers on distribution should not tend to leave out of account the available information on palaeogeography. A concurrence of stratigraphical, geomorphological and geophysical evidence makes it difficult not to believe that the ancient supercontinent of Gondwanaland was a reality, and it seems that its final disruption was complete by the mid-Cretaceous at the latest (King 1958). The details of the former continental assembly and of its disruption indeed provide a causal explanation of the main features of south temperate biogeography. The temperate flora and the invertebrate fauna of the southern continents show unmistakable affinities, evidently the legacy of the ancient continental continuity. In the invertebrate fauna, affinity is closest between South America and southern Australia/Tasmania (Brink 1960). Southern Africa appears to be lacking in such a strong south temperate element. This characteristic is also shown by the flora (Skottsberg 1960), and can be accounted for when it is seen how intimately South America and Australia were linked in the Gondwanaland complex, both physically and climatically, through Antarctica (King 1958).

Africa, however, became separated from the super-continent while it was in a relatively warmer position than were the southern tips of South America and Australia/Tasmania. The antarctic element in southern Africa is therefore not as conspicuous as it is in the sister continents. Further, it seems that as far as the vertebrates are concerned, Gondwanaland broke up so long ago that the present distribution pattern shows little if any of its influence (Darlington 1957).

Temperature

Despite the relatively poor representation of antarctic elements in southern Africa, the existence of a distinctive non-tropical "South African" fauna (Poynton 1961a) indicates that latitudinal zonal temperature has had a profound influence on distribution in southern Africa. The immense importance of zonal temperature as a determinant of distribution is shown by the fact that the differentiation of the world's fauna as a whole into tropical and non-tropical components follows the zonation of temperature remarkably closely. The 18°C midwinter month surface isotherm is a convenient means of describing the limit of the tropical region not only in southern Africa (Poynton 1961b); in the northern hemisphere the 18°C midwinter month isotherm (as shown in Philips' University Atlas 1958) coincides with the conventional division between the tropical and northern faunal regions (Darlington 1957) in all areas except south-east Asia. It also conforms generally to the conventional lines of demarcation between the Patagonian and Brazilian divisions of South America. In Australia the effect of thermal zonation is difficult to perceive on account of the enormous central desert.

The particular importance of temperature is also shown by its evident ability to determine distribution independently of the habitat pattern. This effect is well shown in the area of Lake St. Lucia, Zululand, where an apparently abrupt and general faunal change (Poynton 1961a) takes place in a region which shows no marked changes in the habitat pattern from north to south. There is a gradual increase in the rainfall from north to south along the Zululand coastal region (Niddrie 1951), but this increase could not in itself be supposed to make conditions less favourable for the tropical fauna. The general conformity between the faunal pattern and the thermal pattern indicates that the faunal pattern is ultimately determined by the thermal pattern. However, it is not easy to see why this faunal change should occur so abruptly in an area showing a very even temperature gradient. Evidently the long period of physiographical stability in south-eastern Africa has permitted the development of a faunal balance which is now controlled by the overall thermal pattern, rather than by any localized factors. With fluctuation of the general thermal pattern in the past, there has presumably been a corresponding shifting of the faunal pattern, and over a long period of time this repeated to and fro movement may have gathered the ranges of the individual species into the present overall pattern of abrupt change.

Whatever the actual *modus operandi* of temperature may be, it does seem that zonal temperature resembles the disposition of land in being a very long-enduring feature which divides faunas on a regional scale. Indeed, the latitudinal zonation of temperature is a geographical feature which must have existed before the continental pattern had taken on its present form. At present, sea barriers on the whole tend to divide longitudinally, and thermal zonation latitudinally, and together these two factors have served to divide the world's fauna into phyletically distinctive regions. The historical endurance and phylogenetic consequences of latitudinal zonal temperature and sea barriers, together with their patterning on a global scale, distinguish these two factors from rainfall and vegetation, which determine rather the local and contemporaneous pattern of the habitats than the general conditions of existence. Zonal temperature and sea barriers may consequently be regarded as being "geographical" factors, in contradistinction to the more "ecological" factors of rainfall and vegetation.

Rainfall

On the whole, rainfall appears to affect distribution indirectly, through its influence on the habitat (Bowen 1933; Poynton, in press). Its influence is most commonly felt through the vegetation pattern. Temperature also has this indirect effect, in addition to its direct effect shown by its apparent ability to determine distribution independently of the habitat pattern. The consequences of freezing provide an obvious example of its indirect effect *via* the habitat. However, in southern Africa the importance of the direct effect far outweighs that of the indirect effect which temperature shares with rainfall: in southern Africa temperature and rainfall determine distribution patterns in essentially different ways. Consequently, the lumping of temperature and rainfall together under the term "climate" is most undesirable because, by doing so, the very fundamental differences between the major effects of these two factors are obscured. Broadly speaking, while temperature and the disposition of land are factors which impose a regional and phyletic pattern on distribution, rainfall and vegetation are factors which impose patterns of adaptive convergence within a faunal region. Ecology, which is more concerned with adaptive convergences and their relation to the habitat pattern, is thus more usually concerned with rainfall and the vegetation pattern than is zoogeography, where interest in taxonomic patterns brings the discontinuity of land surfaces and zonal temperature into particular prominence.

Vegetation

If the above reasoning is valid, large-scale faunal patterning which is determined mainly by the vegetation patterning should be treated with a great deal of caution. Such patterning is well shown in the east to west savanna-rainforest differentiation of the fauna in equatorial Africa. This differentiation raises the question of the zoogeographical significance of the pattern, and particularly whether it is as important to a zoogeographer as is the differentiation between the fauna of East Africa and that of the Cape Province. Taxonomically, the difference between the western forest and eastern savanna faunas across equatorial Africa is apparently no greater than is the difference between the faunas occurring in forest and in grassland in eastern Africa itself. This latter difference is clearly one of ecological importance only, and the larger division across the continent appears taxonomically to be a similar difference, only on a larger areal scale. Thus in zoogeographical terms there appears to be a fundamentally unified fauna in equatorial Africa, the cool highlands excepted (Poynton 1961b).

In contrast, the difference between the fauna of the Cape Province and that of East Africa is taxonomically marked (Poynton 1961a), and is consequently of great zoogeographical importance. Ecologically, however, the north-south differences are on the whole not as marked as the east-west differences, and indeed the complex eastern coastal biome seems to run virtually uninterrupted from East Africa southwards to Pondoland: or at least appeared to do so before the advent of the European settlers. Africa south of the Sahara thus possesses a very marked ecological but poorly marked zoogeographical differentiation from east to west, and a very marked zoogeographical but less marked ecological differentiation from north to south. This dualism in the pattern is evidently due to the differential effect of zonal temperature on the one hand, and the effect of rainfall acting through the vegetation pattern on the other.

Conclusion

It is concluded that the grouping of temperature and rainfall into the single factor "climate" is heuristically valueless and dangerous, and should be avoided. The environmental factors determining distribution seem rather to divide across the term "climate", and separate out into (i) sea barriers and temperature, which are of particular zoogeographical importance

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since they have historical and phylogenetic consequences, and (ii) rainfall and vegetation, which determine more the contemporaneous pattern of the biomes, and whose effects are evident more in the adaptive ecological types than in the phyletic constitution of the fauna.

In the extremely diversified environment of southern Africa, where a single species may be restricted in one part of its range by hot arid conditions, and in another part by cool conditions although the rainfall is favourable, precision in considering the effects of the various environmental factors is of prime importance. The general problems of the control of distribution patterns in southern Africa need to be given far more attention than they have been given in the past, for it is only through concerted work that progress can be made in this vastly complex subject.

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DISCUSSION

- Dr. Winterbottom: Ornithologically there is more resemblance between any given vegetation type in the tropical and temperate regions than there is between different types in the same region. The fundamental distinction amongst birds is between forest and non-forest species.
- Dr. Poynton: Is it really easy to differentiate in birds between mere taxonomic differences on the one hand and systematic differences of phylogenetic significance on the other?
- Dr. Winterbottom: No; it is almost impossible.
- Dr. Bigalke: We must be prepared to consider homoiothermal and poikilothermal animals separately as they may differ in their reactions to temperature.
- Mr. Davis: In the Muridae, ecological factors seem to give the best solution of problems of distribution on present knowledge, though it may be possible to fit these into patterns derived from systematics at a later date.
- Mr. Atwell: Has the effect of man—in extirpation especially—as an ecological factor been given sufficient consideration? For instance, the present distribution of the squarelipped rhinoceros might give rise to quite erroneous theories if we did not know the history of it.
- Dr. Poynton: I agree, and think that we should try to reconstruct on the basis of patterns in groups in which the distribution is not much affected by man.

- Dr. McNae:* Dr. Poynton has used the word "ecology" in three different senses, without defining it. He should be more precise in using this term if he is to make his ideas precise.
- Dr. Poynton:* I agree that in speaking to my paper, I have used the word loosely, but I have been defeated by the absence of adequate terminology; I have experienced difficulty in finding words to fit certain concepts, for instance, to describe "sea-barriers - temperature" and "vegetation & rainfall", and would like to invite ideas.
- Dr. McNae:* Arising out Mr. Attwell's question, it has recently been suggested that savanna is a degradation product, induced by man, and not a natural environment. I think that more consideration should be paid to this.
- Dr. Stuckenberg:* It is generally accepted that most of the ungulates probably evolved in savanna country, which is therefore likely to have existed for a considerable time.